

# Effects of phylogeny and locomotor style on the allometry of body mass and pelvic dimensions in birds

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## Abstract

The pelvic girdle provides physical support and attachment for the hind limb musculature. In birds there is variability in pelvic morphology across different orders and this has been used as evidence for various types of locomotion. However, the morphological variation of pelvic bones has yet to be studied systematically in birds. Therefore, we investigated basic allometric relationships among female body mass (as a size proxy) and various pelvic measurements in a phylogenetic context. We also examined in detail the interrelationships among various pelvic measurements. Also considered were the effects of broader taxonomic relationships at the level of order, with further examination of the influence of style of terrestrial locomotion on the allometric relationships. Positive relationships were initially found among all pelvic linear measurements and female body mass (FBM). The relationships among measures of pelvic width and FBM were isometric whereas those between pelvic length and FBM showed positive allometry. Also, FBM explained more of the variance in pelvic length than in width. Similarly, the angle of the pelvis had a significant negative relationship but FBM only explained a very low proportion of the variation in pelvic angles. In general terms ANCOVAs showed that the effect of FBM was smaller than the effect of locomotor style in this species set. Both the synsacrum and pelvic girdle play roles in weight support and therefore scale in proportion to body weight accordingly. All three parts of the pelvis (ilium, ischium and pubis) are attached around the acetabulum and also provide muscle attachment points, so it might be expected for them to scale in a similar manner. Increased angulation of the pelvis is linked to order which employ their hind limbs in feeding, perching and running although FBM also explains a very low proportion of the variation in pelvic angle. Muscle attachment and the confines on morphology presented by locomotion explain much of the variation exhibited by the relationships among pelvic measurements.

**Keywords:** allometry, bird, locomotion, pelvis, phylogeny,

## Introduction

Extant birds exhibit a wide range of body weights, sizes and proportions (Frasier, 1984; Hone et al., 2008; Field et al., 2015), with the largest birds being flightless and cursorial presumably because flapping-powered flight imposes constraints on the weight that flying birds may attain. The linear dimensions of long limb bones in birds exhibit a significant positive correlation with body mass, and therefore such dimensions can be used to estimate body mass when direct measurements are not possible (Maloiy et al., 1979; Alexander, 1983; Anderson et al., 1985; Campbell & Marcus, 1992; Egi, 2001; Field et al., 2013). In their study of Cope's rule (increase in body

size through time) in Mesozoic birds, Hone et al. (2008) demonstrated that the length and diameter of both the femora and tibiotarsi correlate significantly with body mass. Most recently, Kilbourne (2014) reported that the masses of hind limb segments (femur, tibiotarsus, tarsometatarsus and phalanges) show a positive allometric relationships with body mass. However, the limb bones are not the only part of the musculo-skeletal system required for terrestrial locomotion. In particular, the pelvic girdle provides physical support and attachment for the upper limb musculature. There seems to be variability in the overall morphology of the pelvis across different bird orders and this has been correlated with egg shape (Rensch, 1949; Warham, 1990). More commonly pelvic morphology has been used as evidence for various types of locomotion. For instance, Hinić-Frlog and Motani (2009) investigated morphological correlates of aquatic locomotion in the pelvic girdle and limb of various extant and fossil birds. Although studied in some groups, e.g. rails (Gruiformes; Bogdanovich, 2014), the morphological variation of pelvic bones has yet to be studied systematically in birds. The allometric relationships between the pelvic bones and body mass have been reported for a wide range of species as part of a wider study of the factors affecting functional morphology of the pelvic limb (Stoessel et al., 2012). However, other measures of the characteristics of pelvic shape, e.g. relative position of the acetabulum, have not been investigated, and the effects of order and locomotor style have not been considered in previous studies.

In this study, we investigated basic allometric relationships between female body mass (as a size proxy) and various pelvic measurements in a phylogenetic context, so as to control for the degree of non-independence introduced by evolutionary relationships (Garland et al., 2005; Felice & O'Connor, 2014). Moreover, we examined in detail the interrelationships among various pelvic measurements. Our regression analyses were phylogenetically constrained but we also considered the effects of broader taxonomic relationships at the level of order, which have been shown to impact on allometry in a range of other allometric relationships in avian reproduction (see Birchard & Deeming, 2015). Finally, given that species from different orders can occupy similar ecological niches across taxonomic classifications, this study also examined the influence of style of terrestrial locomotion on the allometric relationships. Our rationale for this is that pelvic size and shape are likely to better reflect evolutionary pressures derived from locomotion rather than reproduction. We tested the hypotheses that linear dimensions of bird pelvis will reflect both taxonomic and ecological factors, such as locomotor style.

## Methods

### *Pelvic bone data*

Data were collected from skeletal specimens digitally photographed in the following institutions: Wollaton Hall, Nottingham; The Alfred Denny Museum, University of Sheffield; The Grant Museum of Zoology, University of College London; The Natural History Museum, Tring. Photographs were taken with a 12.1 megapixels Canon Powershot digital camera mounted on a tripod. Measurements were either taken directly from the specimens or collected digitally in tpsDig Version 2.17 (Rohlf, 2008).

Pelvic measurements were collected from 146 specimens (one per species) in 15 orders (with the Palaeognathae combined into one category - ratites) encompassing a wide spectrum of body sizes and locomotory abilities (see Table 1). The following pelvic measurements (Stoessel et al., 2012; Endo et al., 2012) were collected with digital Vernier callipers ( $\pm 0.01\text{mm}$ ): iliac length (IL in Fig. 1) is the distance between the most cranial extremity of the iliac crest and the most posterior extremity of the post-acetabular ilium. Synsacral length (SL in Fig. 1) is the distance between the most cranial and most caudal median points of the synsacrum. Acetabular width

(AW in Fig. 1) measures pelvic width between the anterodorsal margins of the acetabula. Antitrochanter width (ATW in Fig. 1) measures pelvic width between the anterodorsal tips of the antitrochanters. Pubis measurements were excluded in the analysis because in many specimens one of or both pubes were incomplete. Moreover, rarely in birds do the pubes fuse distally and we reasoned that the distal ends of the pubes were most likely to be subject to post mortem alterations.

Additional measurements collected digitally using the “Measure Mode” tool in tpsDig on photographs of pelvises in right lateral view were as follows: pre-acetabular ratio (PAR), *i.e.* ratio of pre-acetabular length of the ilium divided by the total length of the ilium. Therefore, the pre-acetabular length (orientated horizontally in the photographs) is the distance between the anterior extremity of the ilium (see Fig. 1) and the approximate mid-point of the acetabulum. Acetabular depth (ACD) was measured as a proportion of the total depth of the pelvis from the most dorsal margin of the ilium to the most ventral point of the acetabulum, using the posteroventral tip of the ilium as the most ventral point. Pelvic angle (Angle, in degrees) was measured with the dorsal aspect of the pelvis held horizontal and lines were drawn from the most anterior tip of the ilium to the posteroventral point of the pubis (Fig. 1). For the angle measurement, a digital box was drawn around the pelvis to mark measurement points, and the angle was measured using the “Angle Mode” in tpsDig.

Previously published data from a wide variety of literature sources (collated by Deeming et al., 2006; Deeming, 2007a, 2007b) was used for mean female body mass (FBM, in grams) for each species. FBM has been shown to be a reliable size proxy in studies of basic allometry of pelvic measurements and bird size (Rising & Somers, 1989). In order to quantify the pattern of distribution of pelvises belonging to different functional categories of birds, species were grouped according to hind limb use. The categories for water birds were taken from Ibáñez & Tambussi (2012) whereas other categories were based upon several sources (Campbell & Lack, 1985; Ogilvie & Pearson, 1994; Felice & O’Connor, 2014). The distribution of locomotory style across orders is reported in Table 1.

### *Data analysis*

Linear regressions were performed in the R environment for statistical analysis (R Core Team, 2014) using version 3.1-1 of the ‘ape’ package (Paradis et al., 2004). All data were  $\log_{10}$  transformed prior to analysis to normalise variances. Although sexual dimorphism in body size is commonly found amongst birds (Schnell et al., 1985) a one-way ANOVA, performed in R using the ‘ape’ package, both with and without phylogenetic control, showed no significant differences among male, female and unknown specimens in any of the pelvic measurements ( $P > 0.05$  in all cases). As a result, data were combined in subsequent analyses. Phylogenetically controlled linear regressions were conducted with the “pglm” command set to estimate Pagel’s  $\lambda$  (Pagel, 1999) using branch lengths provided by the phylogenetic tree. The chosen tree was the first in a list of 10,000 trees output with the ‘Hackett All Trees’ option on Birdtree.org (Jetz et al., 2012). Regressions were performed to explore the relationships 1) among FBM and pelvic dimensions and 2) among pelvic dimensions.

All other statistical analyses were performed in Minitab version 17. Effect of order was assessed using one-way ANOVA with a *post hoc* Tukey test. Analysis of covariance (ANCOVA) was used to analyse the effect of order on 1) pelvic measurements using FBM as a covariate, and 2) pelvic measurements using other pelvic measurements as covariates. Finally, one sample *t*-tests against a predicted value of 0.5 were used to examine the extent to which the acetabulum differed from an off centre position both dorsoventrally and antero-posteriorly in

each order (*i.e.* if either PAR or ACD values were significantly more or less than 0.5 they were not situated centrally within the pelvis).

Principal component analysis (PCA) based on a correlation matrix was used to further investigate pelvic characteristics in the different orders and locomotory groups. Principal components were calculated in Minitab based on IL, AW, ACD, PAR and Angle. Because of the high correlation between IL and SL, and AW and ATW, SL and ATW were not included in the PCA. Levene's tests were used to investigate homogeneity of variances for PC values for the different orders and locomotory categories. Kruskal-Wallis tests were used to investigate the effect of order and locomotory style on PC1 and PC2 individually, and General MANOVA was used to test PC1 and PC2 in combination. Spearman's rank correlation was used to investigate the relationships between PC1 and PC2 with body mass.

## Results

### *Variability in pelvic shape*

Observations showed that the pelvic girdle morphology is highly variable among bird taxa. This variability extends not only to the size and shape of the individual osteological elements but also to their degree of fusion. We feel that it is useful to describe the extremes of the spectrum of pelvic morphology that we observed, such as are typified by the Strigiformes and the Podicipediformes

The pelvic girdles of the Strigiformes were overall quite uniform in their shape. The barn owl (*Tyto alba*) has a dorsally squat and short pelvis (Fig. 2). The pre-acetabular ilium makes up a much larger proportion of the overall pelvis than the post-acetabular ilium and the antitrochanters extend far out beyond the acetabula. The ischium extends some distance beyond the tip of the synsacrum giving the pelvis a curved shape when viewed dorsally. The iliac shields are also broad, meaning that the pelvic girdle has the appearance of becoming quite narrow in front of the acetabulum. Laterally the pelvic girdles of the Strigiformes generally appear triangular in shape due to their significant angulation (Fig. 2). The pre-acetabular ilia are quite flat, with the post-acetabular region angling down sharply towards the ischium and pubis. The pubes themselves are fused to the ischia and vary in their degree of curvature. The ilioischadic foramen is equal to, or larger than, the acetabulum in size.

The Podicipediformes were at the opposite extreme of pelvic morphology. Again morphology is quite similar among species, with the entire pelvic girdle being very thin and elongate (Fig. 3). Using the horned grebe (*Podiceps auritus*) as an example the iliac shields are much more reduced than those in the Strigiformes, and whilst the girdle is thinner anteriorly towards the acetabulum, posteriorly it tapers slowly towards the ischia, which flare out towards the tips. The pubes are also much more visible in the dorsal view and are wider than the widest point of the ilia. Laterally the ilia of the Podicipediformes are curved inwards so that the synsacrum is visible both above and below the iliac shield (Fig. 3). The acetabulum is positioned ventrally and is about half the size of the ilioischadic foramen, and the pre-acetabular region itself is greatly reduced with the post-acetabular region being much more elongate. The pubis and ischium are not co-ossified, and the region between the ilium and the ischium has a pronounced notch.

### *Pelvic dimensions*

The ranges of the various pelvic measurements for the 146 species used in this study are shown in Table S1. These represent 15 orders and the ratites and are approximately two-thirds of recognised orders of birds.

There were significant effects of order on all linear pelvic dimensions with the largest pelvises observed in the ratites and the smallest in Passeriformes (Table S1). Pairwise comparisons between orders are shown in Table S1.

The average Preacetabular ratio (PAR) was  $0.47 (\pm 0.07)$ , *i.e.* the post-acetabular region makes up a slightly larger proportion of the overall pelvic girdle (Table S1) and there was a significant effect of order. There were three orders where this was not the case; Falconiformes, Sphenisciformes and Strigiformes with the PAR exceeding 0.5 and the case of the Strigiformes was as high as  $0.57 (\pm 0.05)$ . The Ciconiiformes, Gruiformes and Galliformes had a PAR approaching 0.5 (see Table S1) and the Anseriformes and the Podicipediformes had a PAR less than 0.5, the latter of which had the lowest value at  $0.31 (\pm 0.01)$ . In addition, one sample t-tests showed that Anseriformes, Sphenisciformes, Podicipediformes and Passeriformes had pre-acetabular ratios that were significantly lower than 0.5, whilst Strigiformes and Falconiformes were significantly higher (Table S2). All other orders were not significantly different from 0.5.

The lateral acetabular depth (ACD) was also significantly different among orders (see Table S1). The acetabulum was situated significantly more ventrally on Podicipediformes than all other orders (Table S1). The Sphenisciformes and Podicipediformes had ACD values which were significantly higher than 0.5, whilst the Anseriformes, Charadriiformes, Passeriformes and Procellariiformes all had ACD values significantly lower than 0.5 (Table S2). All other orders were not significantly different from a value of 0.5.

The pelvic angles among species were shown to be highly variable with a significant effect of order (Table S1). The increase or decrease of the depth of the post-acetabular region can result in pelvises with increased or decreased angulation (respectively). The Passeriformes had the most angular pelvises, which were deeper than those of all orders except the Columbiformes, Falconiformes, Ratites and Strigiformes. The Podicipediformes had the shallowest angle (Table S1).

#### *Allometric relationships with body mass*

Individual positive relationships occurred among FBM and all seven pelvic measurements with the exceptions of PAR and ACD (Table 2). As FBM increased all linear dimensions increased but the two width measures exhibited isometry with exponents ranging from 0.30 and 0.32. By contrast, with exponents of 0.38 and 0.39 the measures of length (Table 2) exhibited significant positive allometry. In effect, as female bird mass increases, their pelvises increase in absolute length but they get progressively relatively longer whilst their widths remained relatively similar.

ANCOVAs revealed that both order as a fixed factor, and LogFBM as a covariate, had significant effects on log-transformed values for both length and width measures (Table 3), *e.g.* AW versus FBM (Fig. 4). There was no significant effect of the interaction for the two measures of length but there were significant interactions for the width measures (Table 3) indicating that whilst heavier birds do have wider pelvises overall they are relatively thinner than those belonging to lighter birds but this was order dependent.

ANCOVAs also indicated that locomotor style as a fixed factor significantly affected length and width measures (except LogAW, which only approached significance) and LogFBM was a highly significant effect (Table 3). There were highly significant interactions between locomotion and LogFBM for Log IL (Fig. 5) and LogSL but not for LogAW and the effect was only just significant for LogATW (Table 3).

LogFBM did not have a significant allometric relationship with LogPAR (Table 2). Both order and LogFBM as a covariate significantly affected LogPAR but the interaction term did not have a significant effect (Table 3). Locomotor style was a significant factor affecting LogPAR but there was no effect of body mass although the interaction was highly significant (Table 3). For instance, grasping birds seemed to have a higher PAR than the foot-propelled divers (Fig. 6).

Similarly, LogFBM did not have a significant allometric relationship with LogACD with its exponent not being significantly different from zero (Table 2). Neither order nor LogFBM as a covariate significantly affected LogACD (Table 3). By contrast, locomotor style was a significant factor affecting LogACD but there was no effect of body mass but the interaction was highly significant (Table 3).

LogFBM had a slightly negative but highly significant relationship with the angle of the pelvis (Table 2); in effect, as a bird's mass increases its pelvis becomes flatter and less triangular in appearance. ANCOVA showed that LogFBM, but not order, had a significant effect on LogAngle; the interaction was also significant (Table 3). This effectively means that heavier orders have less angular pelvises. When considering locomotor style this was a significant fixed factor but LogFBM only approached significance (Table 3). The highly significant interaction term showed that the angle of the pelvis was dependent on locomotor style and body mass.

#### *Interrelationships among pelvic dimensions*

No significant relationship was found between LogIL and LogSL (Table 4). ANCOVA showed that order was not a significant factor but LogIL with no significant interaction (Table 5). A similar result was found for ANCOVA testing the effects of locomotor style (Table 5).

Strong positive relationships were found between LogIL and LogSL and the two width measurements, LogAW and LogATW (Table 4). As the overall length of the pelvis increased when measured by the length of the ilia, so did width when measured at both the acetabulum and the antitrochanter but the negative allometry meant that the pelvic girdles were relatively thinner. ANCOVA with LogIL as a covariate showed that order was a significant fixed factor and both LogIL and the interaction had significant effects (Table 5). By contrast, LogSL was the only factor significantly affecting LogATW when testing for the effect of order (Table 6). By contrast, the effect of locomotor style and both LogIL and LogSL on width measurements were highly significant and in most cases there was a significant interaction term (Tables 5 & 6).

The position of the acetabulum had a more complex relationship with pelvic length. LogPAR was shown to have a small but significant negative relationship with LogIL (Table 4). By contrast, the position of the acetabulum bore no relationship to the length of the synsacrum (Table 4). ANCOVA showed that order was a significant factor, as was LogIL or LogSL, but there was no significant interaction (Tables 5 & 6). By contrast, in all comparisons locomotor style is a highly significant factor - the covariate is not significant but the interactions are (Tables 5 & 6). In general terms the same pattern is seen for pelvic girdle width – there are no significant allometric relationships with LogPAR (Tables 7 & 8). When investigating for effects of order there are few significant effects but locomotor style is a highly significant factor with a significant interaction with width but width measures in themselves are not significant covariates (Tables 7 & 8). The same pattern is seen for the ACD and angle data; there are no significant relationships with LogPAR and only when locomotor style is considered are significant effects and interactions seen (Table 9).

Conversely, the position of the acetabulum dorsoventrally (LogACD) had no significant allometric relationships with any other variable except for LogAngle (Table 4). When testing for the effects of order there are no significant effects observed for any variable (Tables 5-9) with the exception of LogAngle where order and LogACD are both significant (Fig. 7; Table 10) but the interaction term was not. A similar pattern of locomotor style is seen for LogACD (Table 10). The position of the acetabulum seems to be inversely related to the angle of the pelvis (Table 3) and this is affected by taxonomy and ecology.

Finally, the curvature of the pelvis (LogAngle) had a significant negative relationship with LogIL (Table 4). As the ilium increased in length, the angle of the pelvis decreased overall but was relatively more angular. Only the interaction between order and LogIL was significant in the ANCOVA (Table 5). This effect was increased for locomotor style but LogIL was also significant in this model (Table 5). All other relationships with LogAngle were not significant (Table 4) and ANCOVA testing the effect of order produced no significant results with any other variable (Tables 6-9) except LogACD (Table 10). In extreme contrast, ANCOVAs testing the effect of locomotor style on LogAngle showed significant effects of the fixed factor and all other covariates and there was a positive interaction in each case (Tables 5-10).

#### *Principal component analysis*

The first two principal components explained 68.5% of the variance in the data and loadings for PC1 and PC2 are shown in Table 11. Large positive values for PC1 were associated with increasing size of the pelvis whereas large negative values were associated with increasingly large pelvic angles. For PC2 large positive values were associated with large pelvic angles whereas large negative values were associated with higher values for ACD (Table 11). For PC3 the loading showed a large effect of PAR with highly positive values being associated with small PAR values and large negative PC3 values being associated with small values for PAR.

The mean scores for PC1 and PC2 for each order are plotted in Figure 8. Ratites were characterised by large, more angled pelvises whereas Podicipediformes had relatively large pelvises with the greatest acetabular depth. Passeriformes were characterised by relatively small more angled pelvises. Locomotor style also affected the distribution of species with cursorial birds having relatively large angled pelvises whereas both foot-propelled, and wing-propelled diving birds had moderately sized pelvises characterised by deeper acetabular depth (Figure 9). Levene's test indicated that both variance for PC1 and PC2 were not homogeneous for either order or locomotor style ( $P < 0.001$  in all cases). Kruskal-Wallis tests all showed significant effects of order and locomotor style on PC1 or PC2 ( $P < 0.001$  in all cases) and MANOVA tests showed a similar highly significant effect of order or locomotor style on PC1 and PC2 combined (Wilk's lambda 0.300 and 0.115 respectively, both  $P < 0.001$ ). PC1 was significantly positively correlated with female body mass (Spearman's rho = 0.895,  $P < 0.001$ ) but neither PC2 nor PC3 showed any significant relationship with body mass (Spearman's rho = -0.062 and -0.076,  $P > 0.05$ , respectively).

## **Discussion**

### *Allometric relationships with body mass*

With the exception of PAR and ACD, positive relationships were initially found among all linear pelvic measurements and FBM. The relationships among measures of pelvis width and FBM were isometric whereas those between pelvic length and FBM showed positive allometry. These observations are similar to those by

reported by Stoessel et al. (2012). Also, FBM explained more of the variance in pelvis length than in width. Similarly, the angle of the pelvis had a significant negative relationship but LogFBM only explained a very low proportion of the variation in pelvic angles. In general terms ANCOVAs showed that the effect of order was smaller than the effect of locomotor style in this species set.

Hind limb measurements, such as the lengths and widths of the femur and tibiotarsus correlate with body mass (Frasier, 1984; Hone et al., 2008; Field et al., 2015). The pelvic measurements used in this study (with the exception of the position of the acetabulum) were shown to significantly correlate with female body mass. There are a number of studies looking at pelvic measurements and morphology but very few have analysed the relationship between these and body mass in birds. Hertel & Campbell (2007) demonstrated that pelvic width when measured from the acetabula and antitrochanters correlated with body mass. Whilst Stoessel et al. (2012) found similar results in terms of pelvic allometry the emphasis of their study was more on characteristics of the hind limb and body mass.

The length and shape of the synsacrum can vary with maturity and hind limb use in birds (Baumel & Witmer, 1993; Kaiser, 2007; Jadwiszczak, 2014). Kaiser (2007) states that the synsacrum shortens and stiffens the back, and therefore provides stability during flight; this would also appear to be true in non-volant penguins (Jadwiszczak, 2014). It would therefore be expected that as birds increase in size the synsacrum must also increase in size to continue to support the bird's weight adequately. In one study of the evolution of bill size, Hughes (2014) found that synsacrum length increased with positive allometry relative to body mass and this was attributed to the enhanced need for weight support in the overall heavier hornbills. No similar relationship was seen in toucans, and Hughes (2014) suggested that this may be due to their substantially smaller body masses and the fact that they spend much less time on the ground than hornbills.

The three bones of the pelvic girdle, the ilium, ischium and pubis, are fused to the synsacrum (Campbell & Lack, 1985), so it is not unreasonable to assume that they may scale with FBM in similar ways. The ilium and most other pelvic region bones act as points of muscle attachment for the limbs and tail (Gatesy & Dial, 1993; McCracken et al., 1999; Sathyamoorthy et al., 2012), and therefore as the pelvis increases in overall size it would be expected that these points of muscle attachment increase in size also. If avian hind limb bones scale with FBM as previously reported (Hone et al., 2008; Field et al., 2015) then the muscle attachment points for these limbs will also need to scale accordingly. A basic description of the musculature and hind limb can be found in Rosser et al. (1982) and Ibáñez and Tambussi (2012). The pre-acetabular region acts as the main attachment point for the flexor muscles of the femur (*m. iliotibialis cranialis*, *m. iliotibialis lateralis* and *m. iliotrochantericus caudalis*) whilst the muscles attached to the post-acetabular region control the knee-joint (*m. iliofibularis* and *m. flexor cruris lateralis*). Cormorants of the genus *Phalacrocorax* have a more developed post-acetabular region suggesting extensive femur movement, whilst the greater relative length of the post-acetabular region in the grebes *Podiceps* and *Podilymbus* give rise to a more restricted femur movement with strong knee flexion (Ibáñez & Tambussi, 2012).

An increase in pelvic angle, *i.e.* a downward tilt, is seen in birds of prey, parrots and birds with cursorial habits, such as ratites. It has been suggested that this is an adaptation to specialised use of the hind limbs. Campbell & Tonni (1983) compared the pelvic angles (measured between the long axes of the pre-acetabular ilium and the post-acetabular ilium) of *Teratornis merriami* (an extinct vulture-like bird) with a number of species including the California condor (*Gymnogyps californianus*), the golden eagle (*Aquila chrysaetos*) and a number of other



species. However, Campbell & Tonni (1983) found that the pelvis of *T. merriami* ( $165^\circ$ ) was most anatomically similar to that of storks and other birds which employ a cursorial tactic when searching for food. The same angle in *G. californianus* and *A. chrysaetos* was  $25^\circ$  and  $40^\circ$  respectively. The downward tilt of the post-acetabular pelvis in condors and other vultures was suggested by Campbell & Tonni (1983) to be a result of using their feet to hold food items in place whilst feeding. The orders which employ their feet in feeding, running or perching are quite different in terms of body mass, and this may explain why despite a significant relationship, LogFBM explained only a low proportion of the variance in LogAngle.

In an investigation of the ecological factors affecting avian pelvic limb morphology, Stoessel et al. (2012) reported significant relationships among body mass and measures of pelvic width and length. They examined 236 species of the same orders used here with the exception of Strigiformes and also further subdivided species into ecomorphological groups such as aerial, arboreal, swimming, etc. The report presented by Stoessel et al. (2012) does not offer mean measurements for orders, however a cursory glance of the raw data shows their data to be comparable to that presented here. Their slope exponents for width measurements plotted against FBM are comparable to those found here when controlling for phylogeny, whereas the length measurements are more comparable without controlling for phylogeny but less similar overall. We are appreciative that the phylogenetic relationships of birds are under constant revision (e.g. Prum et al., 2015) and our analysis could be impacted by changes in branch lengths between our taxa. However, the effect of controlling for phylogeny was found to be minimum in analyses that compared allometric equations derived from ordinary and phylogenetically controlled regressions (Anten-Houston, 2015). We feel that changes in phylogenetic relationships will have relatively little impact on our regression estimates but we will be investigating further.

Hertel & Campbell (2007) showed significant correlations between acetabular and antitrochanter width and body mass ( $r^2 = 0.64$  and  $0.57$  respectively,  $p < 0.001$  for both). These two measurements of pelvic width were not as strongly correlated with body mass as other measurements used in the study such as femur length or antitrochanter area (Hertel & Campbell, 2007). Hertel & Campbell (2007) attributed this to an effect of hind limb function. For example, a decrease in overall pelvic width is associated with streamlining the body for foot propulsion or diving (Raikow, 1970; Warham, 1990). The relationships between AW and ATW with FBM in our study were stronger than those reported by Hertel & Campbell (2007), even when controlling for phylogeny. However, the exponent values of ATW and AW reported here were low, especially when compared to those of length measurements. This may be due either to the effects of hind limb function as suggested, or the greater need to conserve overall pelvic length more than width. In the case of the pelvis, the long axis provides much of the muscle attachment for the hind limbs (Gatesy & Dial, 1993; McCracken et al., 1999; Sathyamoorthy et al., 2012). As such, we suggest that these muscle attachment points are of greater evolutionary importance (and therefore more conserved across sizes of birds) than pelvic width.

It is not clear why PAR and ACD should have no significant relationship with female body mass. It may be related to the fact that our measurements of PAR and ACD actually give information other than just the depth and elongation of the pelvis. Firstly, they provide information about the position of the acetabulum on the pelvis and therefore the relative position of the legs. Secondly, the PAR in particular provides information about the general size of the iliac shields. The position of the legs is known to be related to locomotion, e.g. the posteriorly placed legs of the loons, grebes and auks (Johnsgard, 1987), and the morphological changes of the skeleton are associated with muscle control and movement (Gatesy & Dial, 1993; Abourachid & Höfling, 2012). The pre- and

post-acetabular regions of the pelvis are considered by Ibáñez & Tambussi (2012) to be highly influenced by muscle attachment and mass. In particular, the pre-acetabular ilium acts as an attachment for the thigh muscles and is therefore related to movements of the hind limb (Hutchinson, 2001). ANCOVA showed that order had a significant effect on the relationship between LogFBM and both LogPAR and LogACD in our dataset; the fact that the orders used in this study (and birds as a whole) demonstrate many different modes of locomotion (Abourachid & Höfling, 2012) may be associated with this. Due to these factors it is more reasonable to assume that PAR and ACD as they are measured in this study are more related to locomotion than to supporting a bird's weight.

Despite a noted link between pelvic angle and locomotory style (Campbell & Tonni, 1983) in birds which employ cursorial tactics when searching for food (detailed above), the relationships between pelvic angle and body mass have not been investigated. Our results have shown that the slight negative relationship between LogAngle and LogFBM is actually significant. The explanation for this may lie with the large variation in weight of those bird species that have large pelvic angles, i.e. the ratites, birds of prey, parrots and passerines. In this study, those groups of birds had similar mean pelvic angles (ratites =  $28.5^\circ \pm 2.6$ , passerines =  $29.0^\circ \pm 0.6$  and Falconiformes =  $27.8^\circ \pm 0.9$ ), had much more disparate values for mean ( $\pm$  SD) body masses ( $25004.3\text{g} \pm 11953.5$ ,  $118.4\text{g} \pm 40.2$  and  $2069.5\text{g} \pm 670.8$  respectively). This is also supported by the results of the ANCOVA, where the interaction term between order and LogFBM had a significant effect on LogAngle.

#### *Interrelationships among pelvic dimensions.*

Both pelvic width measurements showed negative allometric relationships with iliac length and synsacral length. Synsacral length was shown to have no significant relationship with iliac length, and neither did ACD after controlling for phylogeny. PAR had no relationship with iliac length until after controlling for phylogeny although the  $r^2$  of this model was very small (0.05). Lastly, the angle of the pelvis decreased as iliac length increased and iliac length only accounted for 6% of the variation in pelvic angle. Neither the position of the acetabular (PAR and ACD) or pelvic angle showed any significant relationship with synsacral length.

The widths of the pelvis measured from the acetabula and the antitrochanters were highly correlated and isometric. Neither the position of the acetabulum nor the angle of the pelvis showed any relationship to pelvic width. A significant negative allometric relationship was observed between PAR and pelvic angle. As PAR increases so does the pelvic angle, but the pelvis is less angular overall relative to longer pre-acetabular regions. Finally, ACD correlated with pelvic angle in a negative relationship, with a decrease in pelvic angle the more that the acetabulum moves dorsally. These various allometric relationships among avian pelvic measurements have, up until now, gone unexplored.

That pelvic width increases along with length makes a large degree of sense. The long axis of the pelvis, which measures its length, provides the majority of the muscle attachment for the hind limbs (Gatesy & Dial, 1993; McCracken et al., 1999; Sathyamoorthy et al., 2012). Likewise the acetabula provide the attachment point for the femur head (Campbell & Lack, 1985) and so these two dimensions of the pelvis are intrinsically linked. This was demonstrated by their isometric relationship, but it was noted that the relationship between ATW and pelvic length was stronger than for AW. The antitrochanter acts as an additional point of articulation for the femur and its area can be used to predict body mass (Hertel & Campbell, 2007). It also acts to absorb stresses and provide balance during bipedal locomotion, such as can be seen in the ratites, which were the heaviest group of birds in

this study (Campbell & Lack, 1985). It is, therefore, suggested here that ATW and pelvic length scale more closely than AW because of the need of cursorial species for both relatively powerful leg muscles and the support and balance that the antitrochanter and pelvis as a whole provide.

Iliac length and synsacral length exhibited no relationship, which may be due to the fact that the ilia protrude beyond the synsacrum both anteriorly and posteriorly to different degrees depending on order. ANCOVA showed that order had a highly significant effect on the relationship between LogIL and LogSL, and for all orders except the ratites IL was longer than SL. The most obvious explanation for this is the variation in locomotor style between orders requiring different degrees of muscle attachment and therefore dictating pelvic morphology. The muscle attachment points on the pelvis are split into two main sections, the pre- and post-acetabular regions (Ibáñez & Tambussi, 2012). The pre-acetabular region provides attachment for the muscles responsible for the flexion of the femur, whilst the muscles controlling the movement of the knee joint attach to the post-acetabular region. The size of these muscle attachment points varies among locomotor styles (Ibáñez & Tambussi, 2012), and as part of this study IL was measured as from the anterior tip of the ilium to the most posterior tip of the ischium. As such it would be expected that IL would vary greatly among orders which tend to demonstrate different locomotor abilities.

The pelvis acts as an attachment point for the muscles controlling the movement of the hind limb and tail (Gatesy & Dial, 1993; Felice & O'Connor, 2014). Personal observation (MA-H) and PAR measurements showed that in the Falconiformes, Strigiformes, and Passeriformes the ilia extended most posteriorly beyond the synsacrum. Members of these orders particularly spend a large amount of time airborne, and so a great deal of manoeuvrability and stability are required, and effectively attained by the tail skeleton (Felice & O'Connor, 2014). These muscular systems allow for fine tail movements and tail fanning (Baumel et al., 1990; Gatesy & Dial, 1993). In effect the dual shortening of the posterior synsacrum and the elongating of the posterior ilium jointly aid in the tail movements of primarily airborne birds. However, because neither PAR, ACD nor Angle have any significant relationship with SL, it is more likely that it is in fact an elongation of the sections of the ilia and changes in synsacral length are an artefact of this.

The effect of the pygostyle on SL is not clear as it is not included in our dataset; however its morphological relationship with underwater foraging birds has recently been investigated by Felice & O'Connor (2014). They acknowledge that the number of fused caudal vertebrae that make up the pygostyle can differ among species and locomotor groups, as can the general morphology. Felice & O'Connor (2014) used 51 species of Aequornithes (waterbirds) and assigned them to flight and foraging groups (*e.g.* flap-glide or static soar, foot-propelled or wing-propelled). Pygostyle length and shape was shown to differ significantly among groups, with control and manoeuvrability of the tail being suggested as one cause. Given that the muscles controlling the movement of the tail attach to the post-acetabular region of the pelvis and that the pygostyle differs in shape and length significantly, this could also explain why the length of the ilium extends beyond the synsacrum in varying proportions and why IL showed no relationship to SL.

Pelvic angle became relatively shallow as its iliac length increased. Fisher (1945; cited by Campbell & Tonni, 1983) suggested that an increased post-acetabular angle was “an adaptation for bringing [the] musculature more nearly parallel to the vector force required to pull the femur backward”. This is an adaptation seen in birds that use their hind limbs for grasping and predation (Campbell & Tonni, 1983). This was generally the case in this study. Orders, such as Strigiformes, Falconiformes, Columbiformes and Passeriformes, which use their hind limbs

in a grasping or perching manner, had the most angular but also shortest pelvis. Orders with the least angular pelvises tended to be aquatic, and it is possible that this is an adaptation to decrease drag underwater and make the birds more streamlined when moving through the water. The relationship between aquatic locomotion and angulation of the pelvis is also related to musculature. The post-acetabular region is the connection point for muscles controlling the knee-joint (Ibáñez & Tambussi, 2012); and the posterior position of the hind limbs in aquatic species as well the small degree of angulation in the pelvis is likely an adaptation to allow for efficient knee flexion and paddling through or under the water.

The angle of the pelvis had a significant positive relationship with PAR, but a significant negative one with ACD. In effect the angle of the pelvis increases relative to an increase in the pre-acetabular ilia, but decreases in relation to a ventral movement of the acetabulum. A more angular pelvis has been previously suggested as an adaptation in perching or grasping birds for articulating the femur (Fisher, 1945; Campbell & Tonni, 1983). Such birds were also noted as having the largest PARs in this study. This is despite those species having post-acetabular pelvic dimensions that protrude past the synsacrum. As such, it is postulated that a larger pre-acetabular measurement is simply a reflection of a decreased post-acetabular region. For example, the highest PAR scores were only in the region of half the total length of the ilium, the highest being 0.57 (Strigiformes).

ACD was highest in diving birds such as Podicipediformes and Sphenisciformes, but their pelvis angles were also amongst the lowest, the reason for this may likely be streamlining for ease of movement through the water (Warham, 1990; Ibáñez & Tambussi, 2012). Order as a fixed factor and also the interaction term were shown to have significant effects on this relationship in my results. This may be down to the fact that although aquatic species tended to have dorsally located acetabula and less angular pelvises, the style of locomotion they employed to move through the water differed and therefore these two measures were variable between them.

#### *Non-locomotory effects of pelvic shape*

Morphological relationships of the skeleton may reflect ecological or reproductive characteristics of various species groups. For instance, Hinić-Frlog and Motani (2009) and Bell and Chiappe (2011) have used osteology of the pelvic girdle and limb in the interpretation of locomotion in extinct avian species. In a similar way pelvic dimensions have been linked with the size of eggs laid by extinct species of birds (Dyke & Kaiser, 2010; Endo et al., 2011). This last association seems particularly pertinent given that eggs lie ventral to the pelvis during shell deposition (Gilbert, 1979) and so could influence their size and/or shape (see Endo et al. 2011). Given that egg shape in birds is variable and distinct between different evolutionary groups (Deeming & Ruta, 2014) an investigation of the effects of body size on pelvic bone dimensions should yield interesting relationships. Whilst we know that egg mass correlates strongly with female body mass, it is also a function of order (Deeming 2007a). Any study of how pelvic and egg dimensions co-vary will be hampered by a poor understanding of the effects of body size on pelvic dimensions across a wide range of bird species. In particular there needs to be consideration of different ecological and taxonomic niches for birds. This is because it is more likely that egg shape is a reflection of pelvic size and shape, the evolution of which is more likely driven by locomotion rather than reproduction. This study is, therefore, part of a wider investigation into how pelvic size and shape interacts with egg dimensions and shape and sets the scene by describing the allometric relationships of pelvic bone dimensions with body mass in a range of bird species of varying sizes.

### Summary

After controlling for phylogeny, all pelvic measurements except for PAR and ACD (essentially the relative position of the acetabulum) had a significant relationship with FBM. Pelvic angle was negatively correlated with FBM whilst pelvic length and width were both negatively allometric with FBM. Both the synsacrum and pelvic girdle play roles in weight support and therefore scale in proportion to body weight accordingly. All three parts of the pelvis (ilium, ischium and pubis) are attached around the acetabulum and so also provide muscle attachment points, it might be expected for them to scale in a similar manner. Increased angulation of the pelvis is linked to orders which employ their hind limbs in feeding, perching and running. However these same species are variable in their body weight and therefore FBM explains a very low proportion of the variation in pelvic angle. We attribute PAR and ACD to locomotion as they provide details on the general size of muscle attachment points. Muscle attachment and the constraints on morphology presented by locomotion also explain many of the relationships among pelvic measurements.

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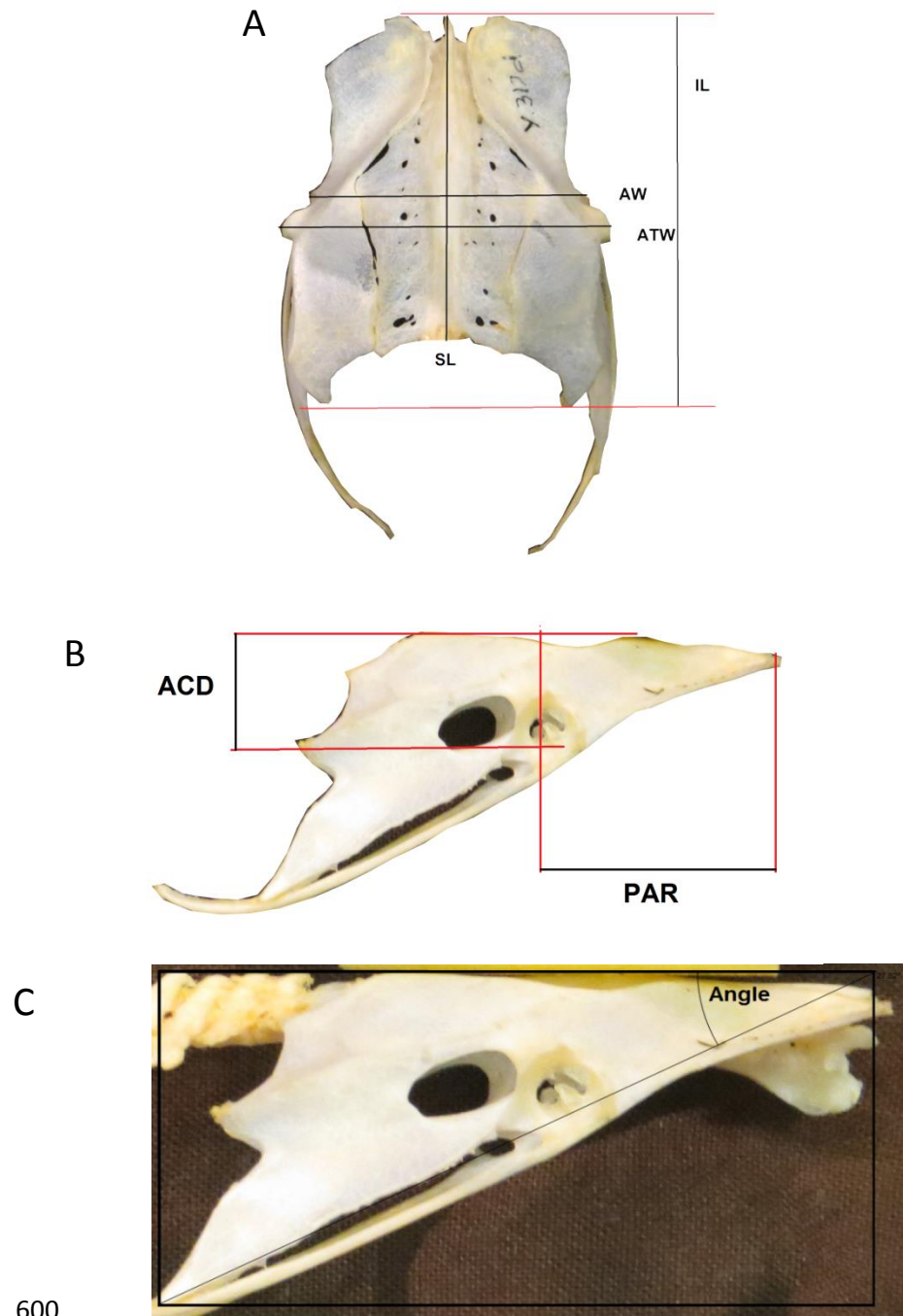
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## Supporting information



**Figure 1.** The pelvic girdle of the rock dove (*Columba livia*) in A) dorsal aspect and B & C) right lateral aspect to illustrate the pelvis measurements used in this study. IL – iliac length, SL – synsacral length, AW – acetabular width, ATW – antitrochanter width. Also collected digitally: ACD – acetabular depth, PAI – preacetabular ilium. Pelvis angle (Angle) was measured by drawing a box around each girdle digitally in tpsDig2 (Rohlf, 2008) to align the dorsal axis.

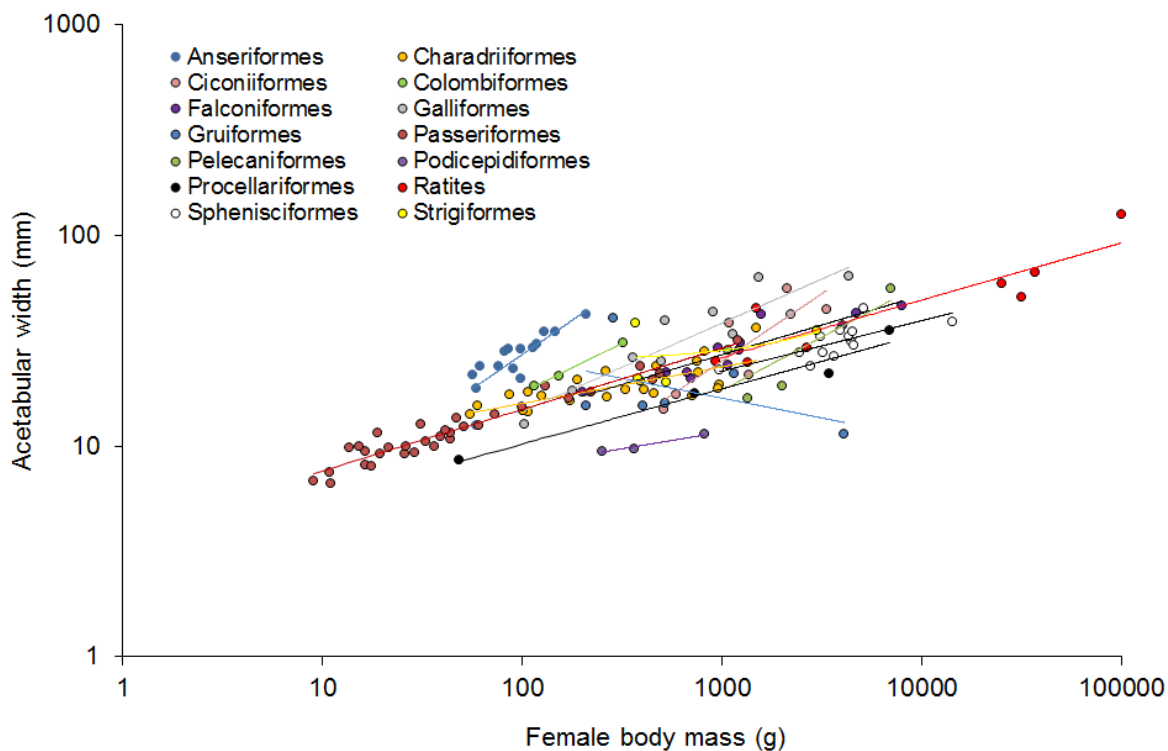




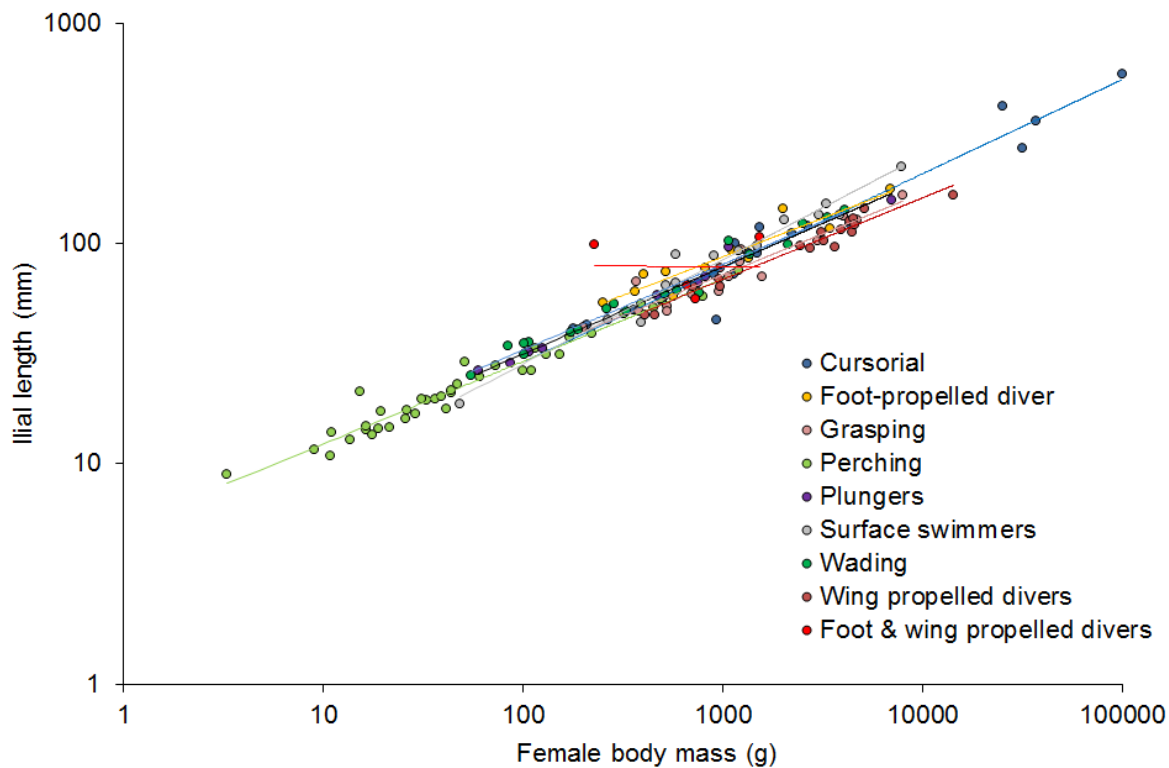
**Fig. 2** The pelvic girdle of the barn owl (*Tyto alba*) is angular in lateral view (left image with anterior to the right) and extremely short and squat in dorsal view (right image with anterior to the top). The postacetabular region is also very reduced.



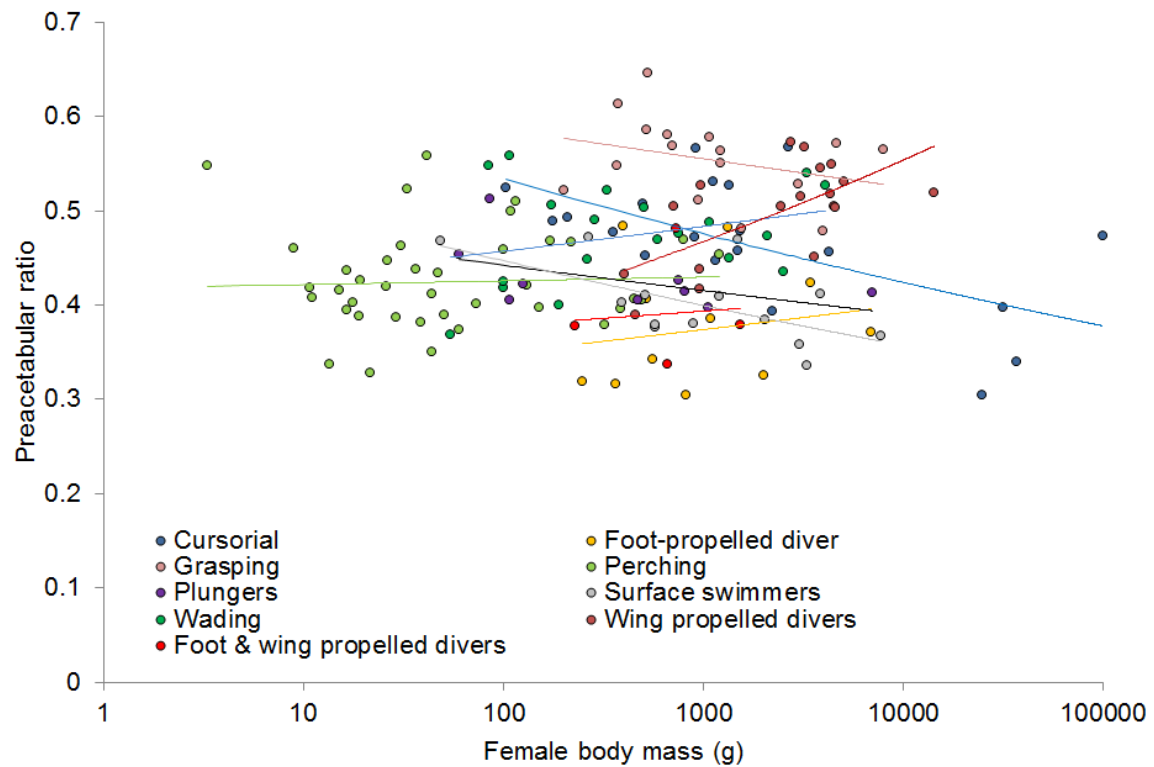
**Fig. 3** The pelvic girdle of the horned grebe (*Podiceps auritus*) is overall extremely elongate. The ilia are very thin and depressed in the lateral view (Top image with anterior to the right) and the ilia and ischia are tapered in the dorsal view (Bottom image with anterior to the right).



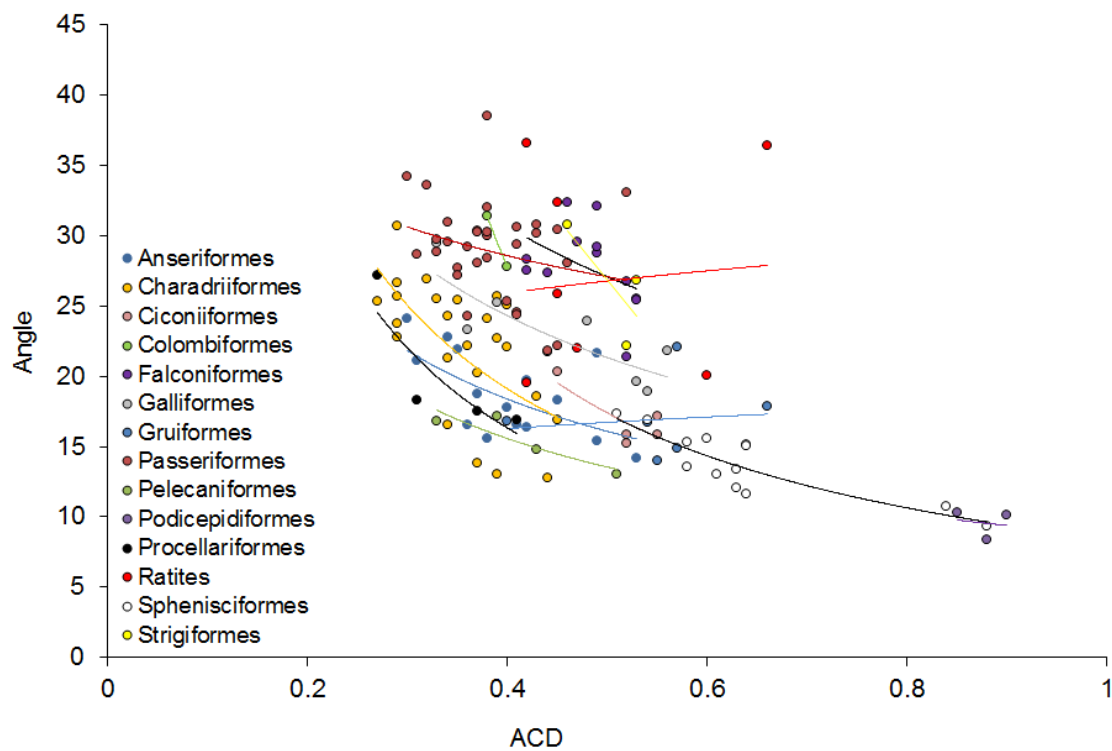
**Fig. 4** Relationship between acetabular width against female body mass with different orders indicated. Note  $\text{Log}_{10}$  axes.



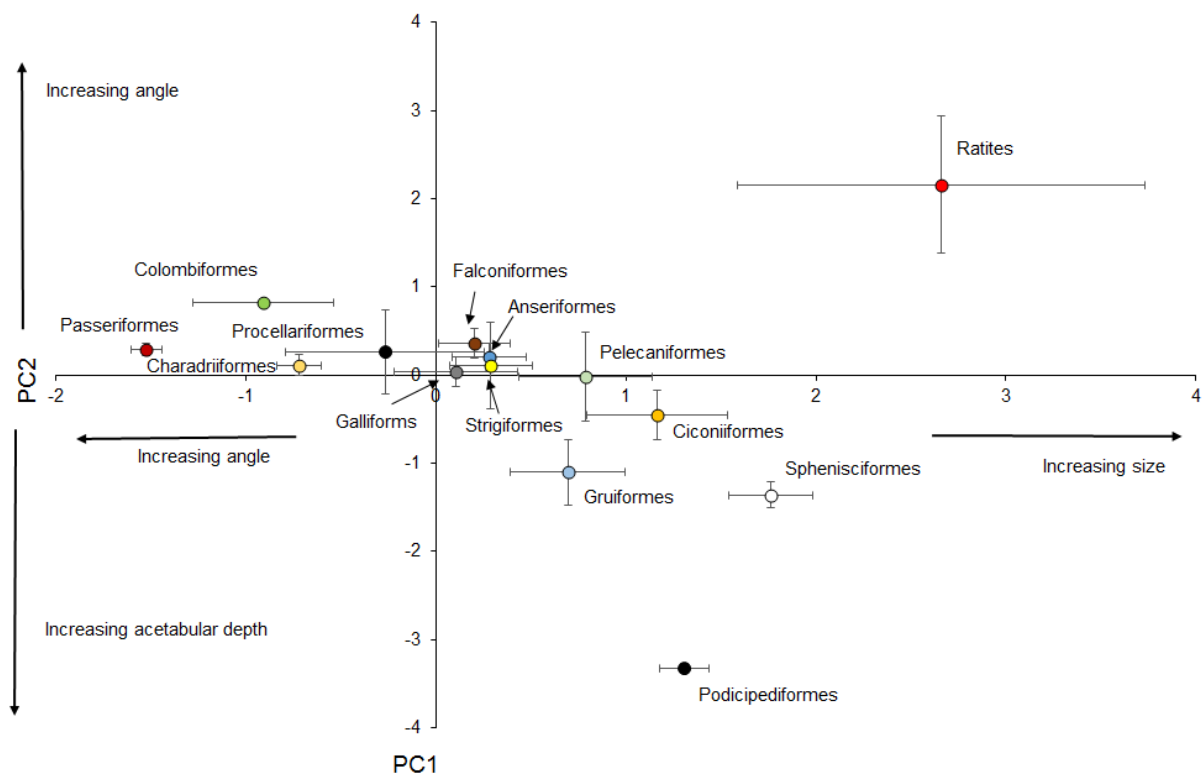
**Fig. 5** Relationship between ilial length against female body mass with different locomotor styles indicated. Note  $\text{Log}_{10}$  axes.



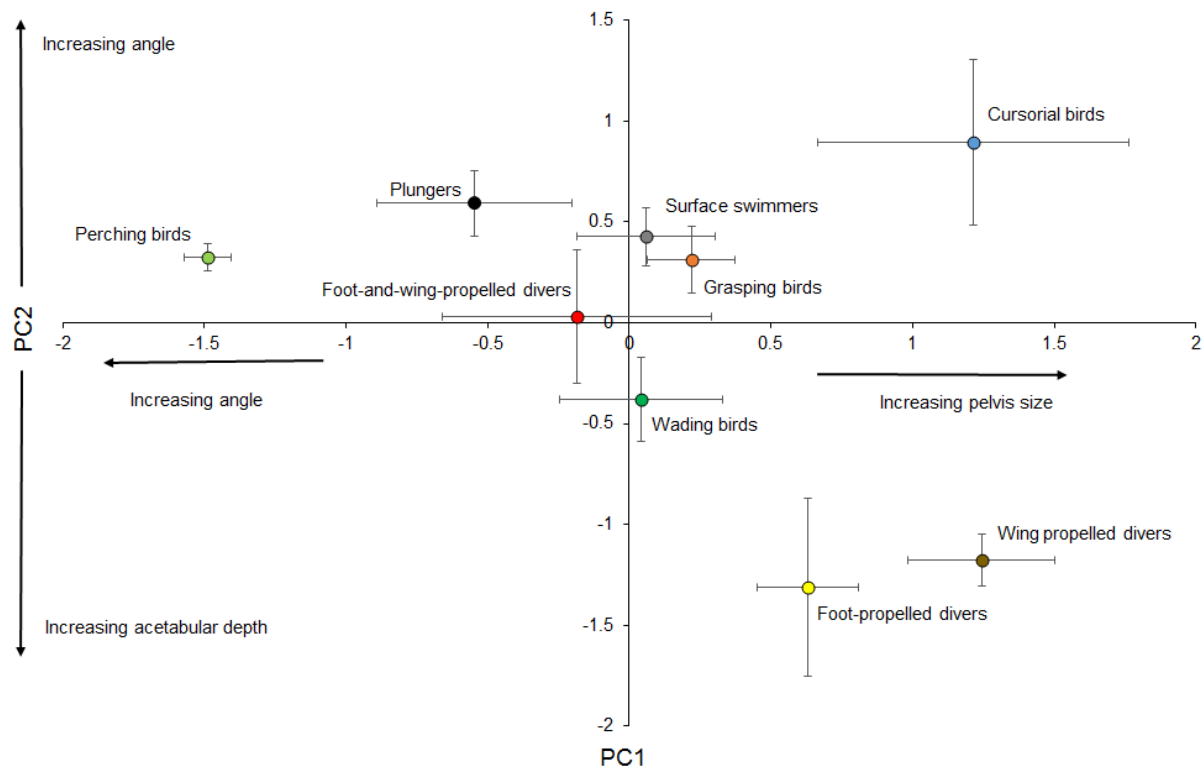
**Fig. 6** Relationship between preacetabular ratio against female body mass with different locomotor styles indicated. Note  $\text{Log}_{10}$  axes.



**Fig. 7** Relationship between pelvis angle against acetabular depth with different orders indicated.



**Figure 8** Plot of the average values ( $\pm$ SE) of the first two principal components for individual orders of birds.



**Figure 9** Plot of the average values ( $\pm$ SE) of the first two principal components for the different locomotory patterns of birds.

**Table 1** Details of species used in morphometric study showing the sample size and colour used for each order in the principal component scatter plots. Also shown are the locomotor groups represented by each order.

Order	Locomotor groups represented	Sample size per group
Anseriformes	Surface Swimmers (SS), Foot-and-wing-propelled divers (FW), Foot-propelled divers (FP).	16
Charadriiformes	Wading (W), Wing-propelled divers (WP), Surface swimmers (SS), Plungers (PL).	24
Ciconiiformes	Wading (W)	6
Columbiformes	Perching (P)	3
Falconiformes	Grasping (G)	12
Galliformes	Cursorial (C)	10
Gruiiformes	Foot-propelled divers (FP), Wading (W), Cursorial (C)	7
Passeriformes	Perching (P)	33
Pelecaniformes	Foot-propelled divers (FP), Plungers (PL)	4
Podicipediformes	Foot-propelled divers (FP)	3
Procellariiformes	Foot-propelled divers (FP), Surface swimmers (SS), Foot-and-wing-propelled divers (FW).	4
Ratites	Cursorial (C)	8
Sphenisciformes	Wing-propelled divers (WP)	13
Strigiformes	Grasping (G)	3

**Table 2** Phylogenetic linear regression estimates for analysis of Log<sub>10</sub> transformed data for LogFBM and Log values for pelvic dimensions. Results are controlled for phylogeny using branch lengths generated by the birdtree.org programme.

Variable	Lambda	Model AICc	Adj R <sup>2</sup>	F	Intercept (± SE)	Slope (± SE)
LogIL	0.54	-391.90	0.92	1688.8 ( <i>p</i> < 0.0001)	0.72 ± 0.04 ( <i>t</i> = 17.35, <i>p</i> < 0.0001)	0.39 ± 0.01 ( <i>t</i> = 41.09, <i>p</i> < 0.0001)
LogSL	0.66	-333.94	0.87	1020.4 ( <i>p</i> < 0.0001)	0.70 ± 0.06 ( <i>t</i> = 12.09, <i>p</i> < 0.0001)	0.38 ± 0.01 ( <i>t</i> = 31.94, <i>p</i> < 0.0001)
LogAW	0.92	-263.88	0.71	358.8 ( <i>p</i> < 0.0001)	0.55 ± 0.12 ( <i>t</i> = 4.43, <i>p</i> < 0.0001)	0.30 ± 0.02 ( <i>t</i> = 18.94, <i>p</i> < 0.0001)
LogATW	0.94	-310.61	0.79	561.0 ( <i>p</i> < 0.0001)	0.61 ± 0.11 ( <i>t</i> = 5.42, <i>p</i> < 0.0001)	0.32 ± 0.01 ( <i>t</i> = 23.68, <i>p</i> < 0.0001)
LogPAR	0.87	-410.73	0.02	3.4 ( <i>p</i> = 0.06)	-0.31 ± 0.06 ( <i>t</i> = -4.96, <i>p</i> < 0.0001)	-0.02 ± 0.01 ( <i>t</i> = -1.83, <i>p</i> = 0.06)
LogACD	0.93	-321.93	0.009	2.3 ( <i>p</i> = 0.13)	-0.40 ± 0.10 ( <i>t</i> = -4.02, <i>p</i> = 0.0007)	0.02 ± 0.01 ( <i>t</i> = 1.51, <i>p</i> = 0.13)
LogAngle	0.95	-319.87	0.07	12.0 ( <i>p</i> = 0.0007)	1.48 ± 0.11 ( <i>t</i> = 13.01, <i>p</i> < 0.0001)	-0.05 ± 0.01 ( <i>t</i> = -3.46, <i>p</i> = 0.0007)

**Table 3** Results of analysis of covariance with order, or locomotor style, as a fixed factor and LogFBM as a covariate for the seven pelvis measurements. Significant effects are highlighted in bold text. All data were Log<sub>10</sub>-transformed prior to analysis.

	Order		LogFBM		Interaction		R <sup>2</sup>
	F <sub>13,113</sub>	<i>p</i>	F <sub>1,113</sub>	<i>p</i>	F <sub>13,113</sub>	<i>p</i>	
LogIL	<b>1.8</b>	<b>0.047</b>	<b>315.4</b>	<b>&lt; 0.001</b>	1.6	0.104	0.971
LogSL	1.4	0.192	<b>207.0</b>	<b>&lt; 0.001</b>	1.5	0.143	0.961
LogAW	<b>2.2</b>	<b>0.015</b>	<b>111.2</b>	<b>&lt; 0.001</b>	<b>2.4</b>	<b>0.006</b>	0.882
LogATW	<b>1.8</b>	<b>0.047</b>	<b>149.3</b>	<b>&lt; 0.001</b>	<b>2.3</b>	<b>0.011</b>	0.920
LogPAR	<b>2.2</b>	<b>0.012</b>	<b>4.8</b>	<b>0.031</b>	1.5	0.122	0.601
LogACD	1.0	0.408	0.6	0.431	0.9	0.574	0.667
LogAngle	1.5	0.124	<b>4.4</b>	<b>0.038</b>	<b>1.9</b>	<b>0.033</b>	0.748

	Locomotor style		LogFBM		Interaction		R <sup>2</sup>
	F <sub>8,128</sub>	<i>p</i>	F <sub>1,128</sub>	<i>p</i>	F <sub>8,128</sub>	<i>p</i>	
LogIL	<b>4.1</b>	<b>&lt;0.001</b>	<b>644.5</b>	<b>&lt;0.0001</b>	<b>4.4</b>	<b>&lt;0.001</b>	0.973
LogSL	<b>5.0</b>	<b>&lt;0.001</b>	<b>439.1</b>	<b>&lt;0.0001</b>	<b>5.7</b>	<b>&lt;0.001</b>	0.963
LogAW	2.0	0.051	<b>175.5</b>	<b>&lt;0.0001</b>	1.0	0.460	0.884
LogATW	<b>3.0</b>	<b>0.004</b>	<b>256.6</b>	<b>&lt;0.0001</b>	<b>2.1</b>	<b>0.039</b>	0.911
LogPAR	<b>3.6</b>	<b>0.001</b>	0.0	0.989	<b>3.1</b>	<b>0.003</b>	0.491
LogACD	<b>9.6</b>	<b>&lt;0.001</b>	2.4	0.122	<b>9.7</b>	<b>&lt;0.001</b>	0.588
LogAngle	<b>4.3</b>	<b>&lt;0.001</b>	3.8	0.054	<b>4.1</b>	<b>&lt;0.001</b>	0.706

**Table 4** The effects of phylogeny on the linear regression analysis of Log transformed data for allometry between pairs of Log values for pelvic dimensions. Results are controlled for phylogeny using branch lengths generated by the birdtree.org programme.

Variable (X:Y)	$\lambda$	Model AICc	Adj R <sup>2</sup>	F	Intercept ( $\pm$ SE)	Slope ( $\pm$ SE)
LogIL:LogSL	6.61e <sup>-5</sup>	101.65	0.009	2.26 ( $p = 0.13$ )	1.47 $\pm$ 0.16 ( $t = 9.49, p < 0.0001$ )	0.13 $\pm$ 0.09 ( $t = 1.50, p = 0.13$ )
LogIL:LogAW	0.97	-263.91	0.72	383.34 ( $p < 0.0001$ )	0.06 $\pm$ 0.17 ( $t = 0.36, p = 0.72$ )	0.73 $\pm$ 0.04 ( $t = 19.58, p < 0.0001$ )
LogIL:LogATW	0.99	-347.74	0.87	965.95 ( $p < 0.0001$ )	0.06 $\pm$ 0.19 ( $t = 0.34, p = 0.73$ )	0.80 $\pm$ 0.03 ( $t = 31.08, p < 0.0001$ )
LogIL:LogPAR	0.88	-414.96	0.05	7.83 ( $p = 0.006$ )	-0.24 $\pm$ 0.07 ( $t = -3.45, p = 0.0007$ )	-0.06 $\pm$ 0.02 ( $t = -2.80, p = 0.006$ )
LogIL:LogACD	0.93	-321.43	0.006	1.78 ( $p = 0.18$ )	-0.42 $\pm$ 0.11 ( $t = -3.85, p = 0.0002$ )	0.04 $\pm$ 0.03 ( $t = 1.34, p = 0.18$ )
LogIL:LogAngle	0.95	-318.17	0.06	10.14 ( $p = 0.002$ )	1.53 $\pm$ 0.12 ( $t = 12.55, p < 0.0001$ )	-0.10 $\pm$ 0.03 ( $t = -3.18, p = 0.002$ )
LogSL:LogAW	0.96	-238.93	0.66	295.18 ( $p < 0.001$ )	0.13 $\pm$ 0.18 ( $t = 0.75, p < 0.45$ )	0.71 $\pm$ 0.04 ( $t = 17.18, p < 0.0001$ )
LogSL:LogATW	0.98	-294.30	0.78	526.40 ( $p = 0.0001$ )	0.14 $\pm$ 0.17 ( $t = 0.80, p < 0.43$ )	0.78 $\pm$ 0.03 ( $t = 22.94, p < 0.0001$ )
LogSL:LogPAR	0.85	-407.82	-0.005	0.29 ( $p = 0.59$ )	-0.35 $\pm$ 0.05 ( $t = -6.37, p < 0.0001$ )	-0.006 $\pm$ 0.01 ( $t = -0.54, p = 0.59$ )
LogSL:LogACD	0.93	-319.64	-0.007	0.009 ( $p = 0.92$ )	-0.34 $\pm$ 0.09 ( $t = -3.50, p = 0.0006$ )	-0.001 $\pm$ 0.02 ( $t = -0.09, p = 0.92$ )
LogSL:LogAngle	0.95	-308.37	-0.006	0.09 ( $p = 0.77$ )	1.33 $\pm$ 0.11 ( $t = 12.04, p < 0.0001$ )	0.005 $\pm$ 0.02 ( $t = 0.29, p = 0.77$ )
LogAW:LogATW	0.35	-442.10	0.93	1807.77 ( $p < 0.0001$ )	0.14 $\pm$ 0.04 ( $t = 3.71, p = 0.0003$ )	0.99 $\pm$ 0.02 ( $t = 42.52, p < 0.0001$ )
LogAW:LogPAR	0.86	-407.75	-0.006	0.22 ( $p = 0.64$ )	-0.34 $\pm$ 0.06 ( $t = -5.15, p < 0.0001$ )	-0.01 $\pm$ 0.03 ( $t = -0.47, p = 0.64$ )
LogAW:LogACD	0.93	-320.07	-0.004	0.43 ( $p = 0.51$ )	-0.38 $\pm$ 0.11 ( $t = -3.51, p = 0.0006$ )	0.02 $\pm$ 0.04 ( $t = 0.66, p = 0.51$ )
LogAW:LogAngle	0.95	-309.93	0.005	1.67 ( $p = 0.20$ )	1.41 $\pm$ 0.12 ( $t = 11.54, p < 0.0001$ )	-0.05 $\pm$ 0.04 ( $t = -1.29, p = 0.20$ )
LogATW:LogPAR	0.89	-411.1	0.010	2.46 ( $p = 0.119$ )	-0.29 $\pm$ 0.07 ( $t = -4.10, p < 0.0001$ )	-0.04 $\pm$ 0.03 ( $t = -1.57, p = 0.119$ )
LogATW:LogACD	0.94	-319.7	0.002	0.35 ( $p = 0.557$ )	-0.38 $\pm$ 0.11 ( $t = -3.40, p = 0.0009$ )	0.02 $\pm$ 0.04 ( $t = 0.59, p = 0.557$ )
LogATW:LogAngle	0.96	-311.1	0.005	1.77 ( $p = 0.185$ )	1.42 $\pm$ 0.13 ( $t = 11.38, p < 0.0001$ )	-0.05 $\pm$ 0.04 ( $t = -1.33, p = 0.185$ )
LogPAR:LogACD	0.94	-319.96	-0.005	0.34 ( $p = 0.56$ )	-0.37 $\pm$ 0.10 ( $t = -3.55, p = 0.0005$ )	-0.07 $\pm$ 0.11 ( $t = -0.58, p = 0.56$ )
LogPAR:LogAngle	0.95	-311.25	0.01	2.96 ( $p = 0.09$ )	1.41 $\pm$ 0.11 ( $t = 12.35, p < 0.0001$ )	0.20 $\pm$ 0.12 ( $t = 1.72, p = 0.09$ )
LogACD:LogAngle	0.94	-353.54	0.27	52.66 ( $p < 0.0001$ )	1.15 $\pm$ 0.09 ( $t = 12.48, p < 0.0001$ )	-0.54 $\pm$ 0.08 ( $t = -7.26, p < 0.0001$ )

**Table 5** Results of analysis of covariance with order or locomotor style as a fixed factor and iliac length (LogIL) as a covariate for the six other pelvis measurements. Significant values are highlighted in bold text.

	Order		LogIL		Interaction		$r^2$
	$F_{13,118}$	$p$	$F_{1,118}$	$p$	$F_{13,118}$	$p$	
LogAW	<b>1.9</b>	<b>0.035</b>	<b>96.04</b>	<b>&lt; 0.001</b>	<b>2.2</b>	<b>&lt;0.001</b>	0.888
LogATW	1.6	0.092	<b>148.9</b>	<b>&lt; 0.001</b>	<b>1.9</b>	<b>0.029</b>	0.928
LogSL	0.3	0.996	<b>448.1</b>	<b>&lt; 0.001</b>	0.4	0.982	0.938
LogPAR	<b>2.2</b>	<b>0.012</b>	<b>4.8</b>	<b>0.031</b>	1.7	0.071	0.601
LogACD	0.7	0.763	0.6	0.428	0.7	0.737	0.661
LogAngle	1.4	0.170	3.8	0.054	<b>1.9</b>	<b>0.042</b>	0.739

	Locomotor style		LogIL		Interaction		$r^2$
	$F_{8,128}$	$p$	$F_{1,128}$	$p$	$F_{8,128}$	$p$	
LogAW	<b>2.7</b>	<b>0.010</b>	<b>202.4</b>	<b>&lt;0.001</b>	1.9	0.072	0.889
LogATW	<b>4.0</b>	<b>&lt; 0.001</b>	<b>325.5</b>	<b>&lt; 0.001</b>	<b>3.3</b>	<b>0.002</b>	0.921
LogSL	1.2	0.294	<b>1242.1</b>	<b>&lt; 0.001</b>	1.4	0.189	0.983
LogPAR	<b>3.7</b>	<b>&lt; 0.001</b>	0.7	0.413	<b>3.5</b>	<b>0.001</b>	0.509
LogACD	<b>7.8</b>	<b>&lt; 0.001</b>	<b>6.0</b>	<b>0.016</b>	<b>8.0</b>	<b>&lt;0.001</b>	0.584
LogAngle	<b>4.5</b>	<b>&lt; 0.001</b>	<b>12.2</b>	<b>0.001</b>	<b>5.0</b>	<b>&lt;0.001</b>	0.739

**Table 6** Results of analysis of covariance with order or locomotor style as a fixed factor and synsacral length (LogSL) as a covariate for the five remaining pelvis measurements. Significant values are highlighted in bold text.

	Order		LogSL		Interaction		$r^2$
	$F_{13,118}$	$p$	$F_{1,118}$	$p$	$F_{13,118}$	$p$	
LogAW	1.2	0.303	<b>54.3</b>	<b>&lt; 0.001</b>	1.4	0.184	0.853
LogATW	0.9	0.525	<b>73.3</b>	<b>&lt; 0.001</b>	1.1	0.336	0.899
LogPAR	<b>2.4</b>	<b>0.006</b>	<b>4.5</b>	<b>0.037</b>	<b>1.8</b>	<b>0.046</b>	0.608
LogACD	0.8	0.672	0.5	0.463	0.9	0.605	0.668
LogAngle	1.2	0.267	2.8	0.096	1.7	0.071	0.738

	Locomotor style		LogIL		Interaction		$r^2$
	$F_{8,128}$	$p$	$F_{1,128}$	$p$	$F_{8,128}$	$p$	
LogAW	<b>4.4</b>	<b>&lt; 0.001</b>	<b>187.6</b>	<b>&lt; 0.001</b>	<b>3.4</b>	<b>0.002</b>	0.873
LogATW	<b>6.5</b>	<b>&lt; 0.001</b>	<b>294.3</b>	<b>&lt; 0.001</b>	<b>5.6</b>	<b>&lt; 0.001</b>	0.906
LogPAR	<b>4.3</b>	<b>&lt; 0.001</b>	0.1	0.755	<b>4.0</b>	<b>&lt; 0.001</b>	0.543
LogACD	<b>7.5</b>	<b>&lt; 0.001</b>	3.6	0.062	<b>7.5</b>	<b>&lt; 0.001</b>	0.586
LogAngle	<b>4.2</b>	<b>&lt; 0.001</b>	<b>9.2</b>	<b>0.003</b>	<b>4.6</b>	<b>&lt; 0.001</b>	0.736



**Table 7** Results of analysis of covariance with order or locomotor style as a fixed factor and acetabular width (LogAW) as a covariate for the four remaining pelvis measurements. Significant values are highlighted in bold text.

	Order		LogAW		Interaction		$r^2$
	$F_{13,118}$	$p$	$F_{1,118}$	$p$	$F_{13,118}$	$p$	
LogATW	<b>6.8</b>	<b>&lt; 0.001</b>	<b>406.9</b>	<b>&lt; 0.001</b>	<b>6.5</b>	<b>&lt; 0.001</b>	0.981
LogPAR	1.8	0.059	2.6	0.108	1.3	0.238	0.574
LogACD	1.3	0.256	0.03	0.869	1.2	0.267	0.677
LogAngle	1.3	0.213	1.3	0.250	0.9	0.530	0.704

	Locomotor style		LogAW		Interaction		$r^2$
	$F_{8,128}$	$p$	$F_{1,128}$	$p$	$F_{8,128}$	$p$	
LogATW	<b>3.9</b>	<b>&lt; 0.001</b>	<b>882.7</b>	<b>&lt; 0.001</b>	<b>4.4</b>	<b>&lt; 0.001</b>	0.971
LogPAR	<b>4.0</b>	<b>&lt; 0.001</b>	0.4	0.523	3.4	<b>&lt; 0.001</b>	0.517
LogACD	<b>11.3</b>	<b>&lt; 0.001</b>	<b>7.6</b>	<b>0.007</b>	<b>10.8</b>	<b>&lt; 0.001</b>	0.629
LogAngle	<b>5.0</b>	<b>&lt; 0.001</b>	<b>8.8</b>	<b>0.004</b>	<b>3.7</b>	<b>0.001</b>	0.723

**Table 8** Results of analysis of covariance with order or locomotor style as a fixed factor and antitrochanter width (LogATW) as a covariate for the three remaining pelvis measurements. Significant values are highlighted in bold text.

	Order		LogATW		Interaction		$r^2$
	$F_{13,118}$	$p$	$F_{1,118}$	$p$	$F_{13,118}$	$p$	
LogPAR	<b>2.1</b>	<b>0.020</b>	3.8	0.055	1.5	0.122	0.592
LogACD	1.0	0.458	0.02	0.875	0.9	0.557	0.666
LogAngle	1.0	0.486	1.7	0.200	0.8	0.712	0.700

	Locomotor style		LogATW		Interaction		$r^2$
	$F_{8,132}$	$p$	$F_{1,132}$	$p$	$F_{8,132}$	$p$	
LogPAR	<b>5.2</b>	<b>&lt; 0.001</b>	0.5	0.494	<b>4.5</b>	<b>&lt; 0.001</b>	0.544
LogACD	<b>12.6</b>	<b>&lt; 0.001</b>	<b>9.9</b>	<b>0.002</b>	<b>11.9</b>	<b>&lt; 0.001</b>	0.641
LogAngle	<b>6.0</b>	<b>&lt; 0.001</b>	<b>9.7</b>	<b>0.002</b>	<b>4.4</b>	<b>&lt; 0.001</b>	0.731

**Table 9** Results of analysis of covariance with order or locomotor style as a fixed factor and preacetabular ratio (LogPAR) as a covariate for LogACD and LogAngle. Significant values are highlighted in bold text.

	Order		LogPAR		Interaction		$r^2$
	$F_{13,110}$	$p$	$F_{1,110}$	$p$	$F_{13,110}$	$p$	
LogACD	0.9	0.608	0.3	0.561	0.9	0.524	0.671
LogAngle	0.6	0.187	1.8	0.187	0.7	0.7	0.693

	Locomotor style		LogPAR		Interaction		$r^2$
	$F_{8,132}$	$p$	$F_{1,132}$	$p$	$F_{8,132}$	$p$	
LogACD	<b>5.4</b>	<b>&lt; 0.001</b>	0.2	0.667	<b>5.1</b>	<b>&lt; 0.001</b>	0.513
LogAngle	<b>2.7</b>	<b>0.008</b>	5.0	0.028	<b>2.52</b>	<b>0.014</b>	0.701

**Table 10** Results of analysis of covariance with order or locomotor style as a fixed factor and acetabular depth (LogACD) as a covariate for LogAngle. Significant values are highlighted in bold text.

	Order		LogACD		Interaction		$r^2$
	$F_{13,110}$	$p$	$F_{1,110}$	$p$	$F_{13,110}$	$p$	
LogAngle	<b>3.0</b>	<b>0.001</b>	<b>4.1</b>	<b>0.044</b>	1.2	0.139	0.789

	Locomotor style		LogACD		Interaction		$r^2$
	$F_{8,123}$	$p$	$F_{1,123}$	$p$	$F_{8,123}$	$p$	
LogAngle	<b>4.8</b>	<b>&lt; 0.0001</b>	<b>47.4</b>	<b>&lt; 0.0001</b>	1.8	0.092	0.806

**Table 11** Variable loadings following principal component analysis for the first three principal components. The standard deviation, eigenvalues and cumulative proportion of variance explained by the PC values are also included.

Variable	PC1	PC2	PC3
Acetabular width	0.578	0.412	-0.092
Iliac length	0.586	0.390	0.112
Lateral acetabular depth	0.415	-0.571	-0.071
Angle	-0.378	0.585	-0.261
Pre-acetabular ratio	0.085	-0.111	-0.952
Standard deviation	1.471	1.122	1.021
Eigenvalue	2.165	1.259	1.043
Cumulative proportion of variance	0.433	0.685	0.893